

NAMALYCASTIS ABIUMA (MÜLLER IN GRUBE) 1871, AN ABERRANT NEREIDID POLYCHAETE OF A GEORGIA SALT MARSH AREA AND ITS FAUNAL ASSOCIATIONS

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ABSTRACT The morphology of the aberrant nereidid *Namalycastis abiuma*, Namanereidinae is described on the basis of material collected 1971-72 and 1976 in the brackish water drainage ditch system of Sapelo Island, Georgia, USA. The systematics of the species is briefly reviewed. The habitat and ecological conditions under which the species lives in these brackish ditches are described.

At various times, *N. abiuma* lives out of water under the bark of trunks and branches of fallen trees. Decaying wood is ingested. It is suggested that future studies should concentrate on the reproductive biology of the widely-spread, mainly tropical populations of what may prove to be not one, but several species of *Namalycastis*. A list of the invertebrate fauna associated with *N. abiuma* is included with notes on these associates.

INTRODUCTION

Namalycastis abiuma (Namanereidinae, Nereidae) was described by Müller in Grube, 1871 as *Paranereis abiuma*. Eleven closely-related species subsequently were described under the generic name *Lycastis*. These species occur in fresh water to brackish or almost fully marine habitats (Wesenberg-Lund, 1958). All species were referred to by the new generic name *Namalycastis* by Hartman (1959), with the comment that all "are believed to refer either to a single species resembling the type, or to closely related, and generically identical forms" (p. 163). Hartman's diagnosis, based on material from Florida, has been generally accepted (Foster, 1972; Gardiner, 1976; Gardiner and Wilson, 1977; Heard, 1975, 1982). Heard (1982) synonymized *Lycastopsis tecolulensis* Rioja, 1946, *L. pontica* Jakubova, 1930, and *L. hummelincki* Augener, 1933, all from North Carolina, Georgia, Florida and Louisiana with *N. abiuma*. *N. abiuma* was reported from Australia by Russell (1962) and *N. cf. abiuma* by Hutchings and Glasby (1985). Although it may seem difficult to accept that Hartman rightly synonymized 11 species of *Abiuma*, considering the diversity of their habitats, it must be noted that only a limited number of systematic characteristics are available, e.g., a pharynx without paragnaths or papillae, reduced parapodia, etc. Therefore, until a more thorough revision of the many forms is available, it seems reasonable to accept Hartman's inclusion of them as members of *Abiuma*.

In this paper, the systematics of *N. abiuma* were briefly reviewed and some morphological details were described based on material from brackish water in Georgia. An

attempt has been made to characterize ecological conditions under which the species occurred, its mode of life, and its faunal associates.

MATERIALS AND METHODS

Site Description

The study area encompassed shallow drainage ditches on Sapelo Island connected to the sea only during periods of extreme high water. A series of ditches, dwindling into pools at low water with different salinity conditions, were chosen for sampling. Populations of *N. abiuma* were found at only two of 10 stations surveyed: Station 1, the main station regularly examined during 1971-72, and Station 10, a supplementary station visited only a few times in 1976 (Figure 1). Station 1 (Figure 2), situated one mile north of the Settlement, was a roadside ditch about 4 m wide and varying in depth from a few cm during dry periods to more than 0.5 m at spring tides. The bottom layer was soft, fine, blackish mud with some smell of hydrogen sulphide. Fallen tree trunks and decaying branches from the surrounding pine forest were piled up in part of the ditch system. Rickards (1968) gave a short description of this study area.

Except for a small patch of *Ruppia maritima* L., present only in 1976, the ditches had no submerged vascular plants. The surface of the mud was covered with a dense brownish layer of diatoms during periods with clear direct sunshine. Tufts of perennial glasswort (*Salicornia virginiana* L.)

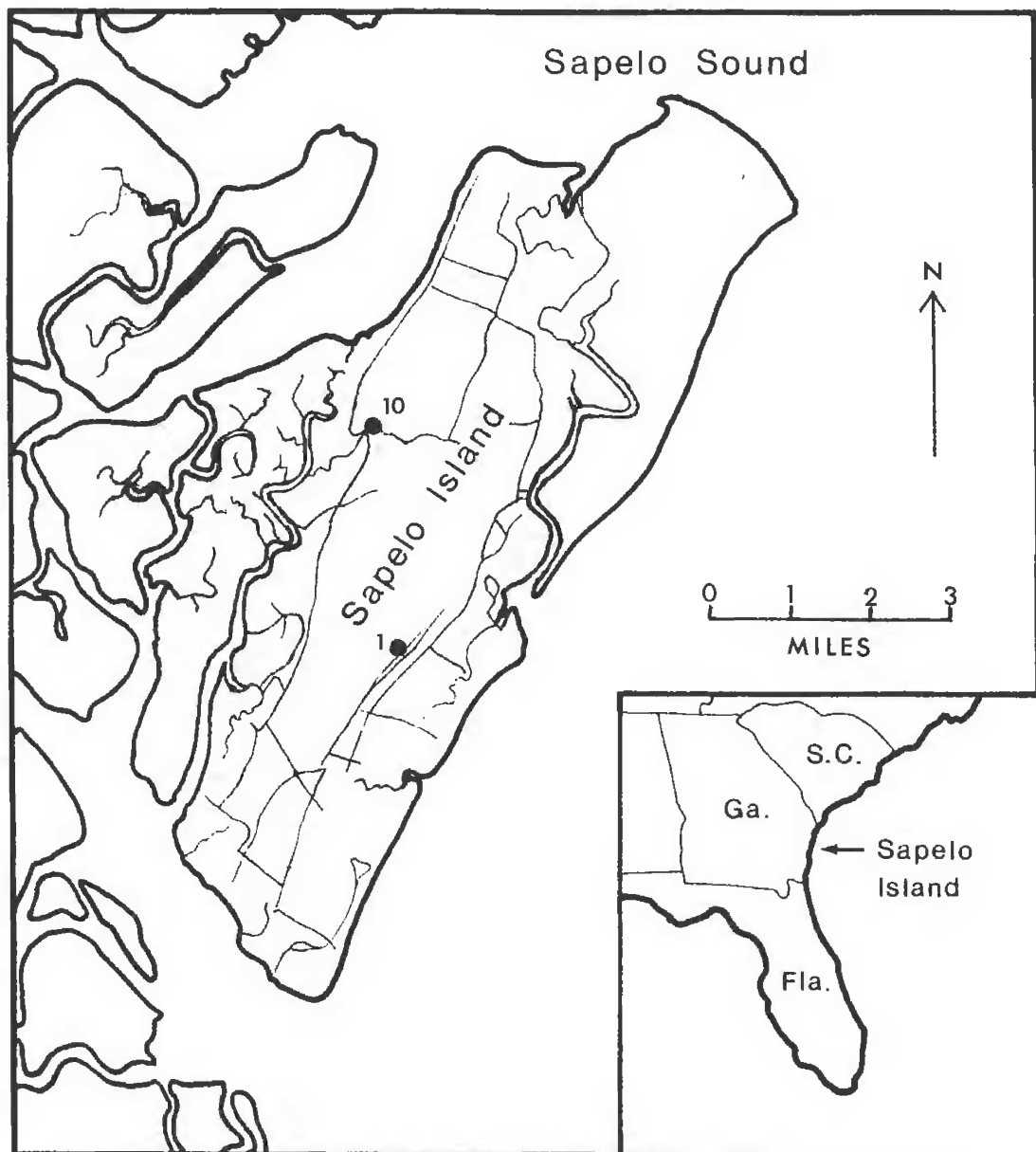


Figure 1. Sapelo Island, Georgia, with tidal creeks, ditches and pools. Numbers indicate sampling stations.

were found on the bank of the ditch near the saltgrass cover (*Distichlis spicata* (L.) Greene). Low bushes of marsh elder (*Iva frutescens* L.) formed a transitional border near the forest in the *Distichlis* marsh clearings. Saltmarsh grass

(*Spartina alterniflora* Loıs.) occurred in some places along the bank edges and often extended across the ditch to form thresholds that often impeded the upstream flow of sea water.



Figure 2. Photograph showing part of Station 1, a roadside ditch with *Spartina* grass along the banks (to the right, opposite the road). Behind the *Distichlis* grass cover bushes of marsh elder (*Iva frutescens*) are bordering the pine tree forest in the background (April 23, 1971).

Station 10 was a ditch located between steep bluffs which ran parallel to the road between the King Savannah clearing and the Bell Marsh near the High Point road. It was surrounded by dense forest. The steep banks of the ditch reached 2 m above the bottom. The bottom sediment was virtually clean sand with plant remnants and scattered *Spartina*. The banks were topped with a dense growth of marsh elder. The ditch was nearly dry during sampling periods. Direct access to sea water gave this ditch a regular tidal cycle.

Salinity

Salinity was measured with a T/C refractometer (American Optical Corp.). Salinity at Station 1 varied greatly according to the irregular rainfall pattern. During most of 1971-72, the salinity varied from ca. 10‰ to ca. 30‰, but drought combined with high air temperature and intense sunlight raised the salinity to 56 in June 1971. However, heavy rains in June and July reduced that salinity to 4‰ within a few days.

In contrast, 1976 was an extraordinarily dry year. At Station 1 from March 13 to April 16, total precipitation was ca. 27 mm (seasonal norm 182 mm). The ditch became almost dry in April, and the remaining stagnant pools became hypersaline at ca. 80‰. But on April 12, a single intrusion of sea water at a spring tide raised the water level to 40 cm and lowered the salinity to that of normal sea water. It appears that fluctuations in salinity over a range of ca. 20‰ are a usual occurrence in spring and early summer. The 80‰ event represents an extreme that the fauna of the ditches must endure occasionally, possibly by retreating to the underbark refuge out of water. This may present other stresses, such as high temperature and the risk of desiccation.

Temperature

Temperatures were measured from April to August 1971 with a mercury thermometer. From late September 1971 to early February 1972, water temperature was measured each week with a permanently submersed maximum-

minimum mercury thermometer that showed the temperature range during the past seven days. From March 14-27, the temperature range was measured continuously with a Grant Miniature Temperature Recorder with six channels registering the air temperature, water surface temperature in the middle of the ditch, water surface temperature near the bank, temperature near the bottom, temperature 1 cm in the mud bottom and temperature 15 cm deep in the mud with a water level ranging from 0.5 to about 40 cm (Figure 3). Rainfall records for 1971-72 were obtained from the meteorological station of the University of Georgia Marine Institute. During the 1976 sampling, precipitation was checked by a rain gauge placed on the ground close to Station 1. Water level was measured daily against a measuring rod placed in the ditch (Figure 2).

The temperature range at Station 1 was very large, both seasonally and daily, influenced by changes in air temperature and solar radiation. After a period of rhythmic fluctuations in April and May 1971 varying between 22°C and 32°C, the hottest period in the 1971-72 study came in June and lasted through September, with a peak of nearly 37°C in June. A more precise estimate of the temperature range was achieved with the introduction of regular maximum-minimum temperature recording of the ditch system water from September 26 through the rest of the research period. A minimum of 0°C was recorded in January 1972.

From March 14-27, 1976, the water level of the pool in Station 1 varied between 10 and 27 mm and the temperature ranged between 12°C and nearly 31°C, never attaining the low level of the air due to the strong solar radiation

(Figure 3). What may be more important is the fact that the narrower temperature range in the mud (15°C to 26.5° at 1 cm depth; 20° to 30°C at 15 cm) might enable some mobile animals to survive under extreme environmental conditions by burrowing into the mud. However, such an escape may subject them to anoxic conditions, and *N. abiuma* was never actually found in the mud in this study.

NAMALYCASTIS ABIUMA

Descriptive Notes

Mature specimens measure about 50 to 100 mm in length, with up to 170 setigers. Body with two, not distinctly separable sections. Anterior third to half rather slender and cylindrical with relatively few segments, rest of body becoming flattened posteriorly, with segments increasingly shorter. Living animal translucent, unpigmented. Color determined by contents of red blood, increasing in intensity posteriorly. Dorsal surface somewhat glossy in reflected light. Epidermis of each segment with fine transverse wrinkles (Figure 4). Prostomium trapezoidal, anteriorly incised, with short median groove. Two small conical antennae and two conspicuous, broad palps with distinct palpostyles; the palps are rhythmically extended when the worm crawls. Posterior part of prostomium broader with two pairs of eyes, black in reflected light, the outer eye on each side larger (Figure 4). Four pairs of tentacular cirri, the hindmost pair longest. First segment achaetous. Pharynx strongly built, without paragnaths or papil-

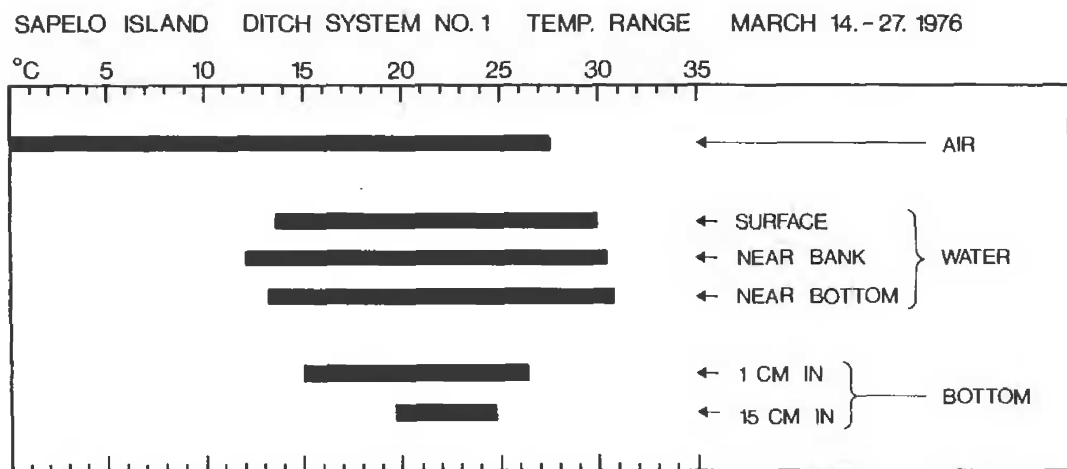


Figure 3. Temperature range in air and ditch at Station 1, Sapelo Island, Georgia, March 14-27, 1976. Measured continuously during this period with a six-channel temperature recorder. All measurements, except "near bank", made over and in the central and deepest part of the ditch. The "bank" channel was at the surface near the water edge. Depth during recording from 10 to 27 cm, falling to 9 cm.

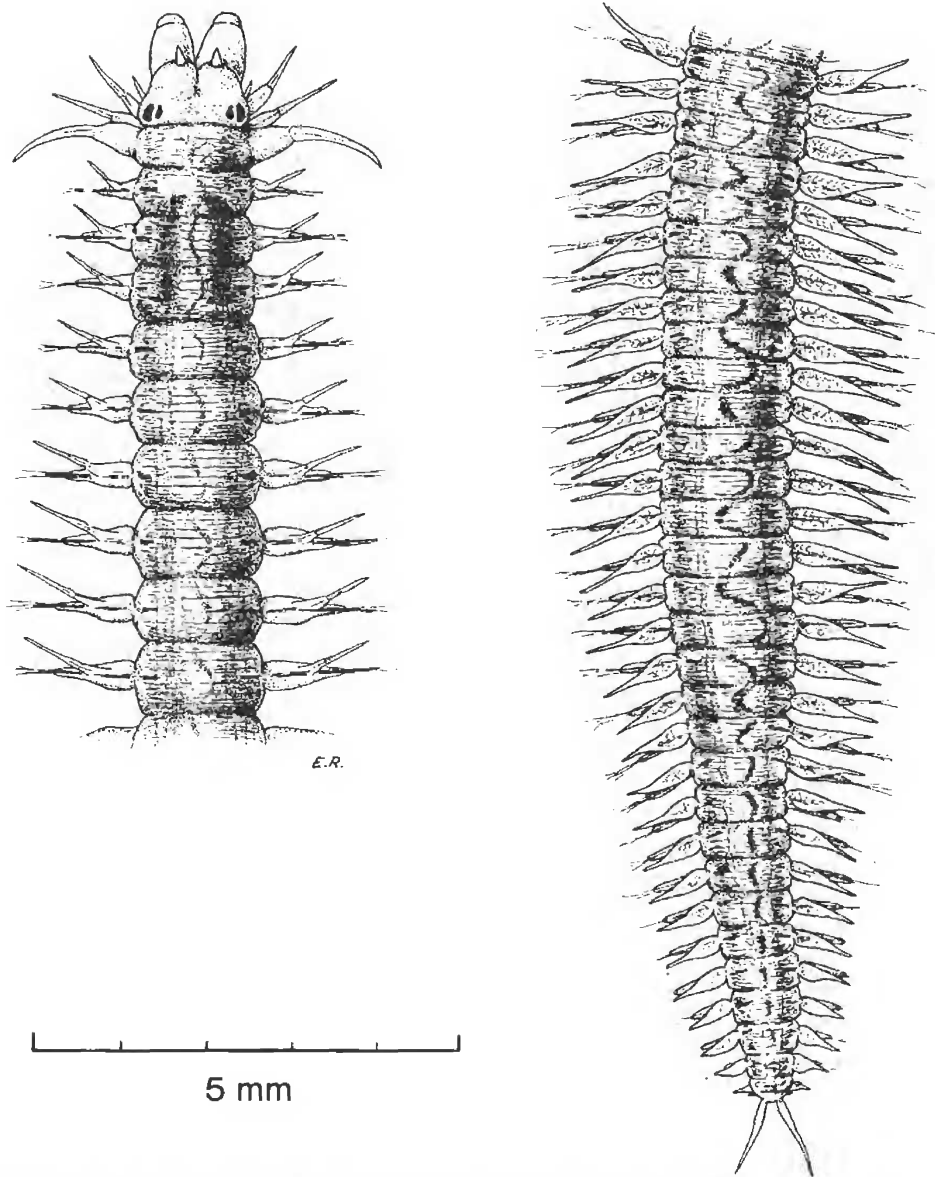


Figure 4. *Namalycastis abiuma* (Müller in Grube, 1871). Adult specimen from Station 1, Sapelo Island, Georgia, November 1971, showing anterior and posterior ends of the body. Drawn from life with the aid of a camera lucida.

lae, with two dark brown, strong chitinous jaws (Figure 5). Jaws concave, almost spoon-shaped, in living animals visible through the first 2-3 setigers; median edge of each jaw with a row of teeth. The terminal tooth, somewhat separated from the row of teeth, slightly larger than the rest. Each jaw with fine growth rings. Parapodia sub-biramous with noto- and neuropodial aciculae,

dark brown or almost black. Notopodia normally reduced, without setae except for an occasional, slender heterogomph spiniger. Dorsal cirri anteriorly slender and small, conically shaped; posteriorly long, flattened leaflike in structure with constricted terminal tips and a very rich supply of fine capillary vessels. Ventral cirri small throughout.

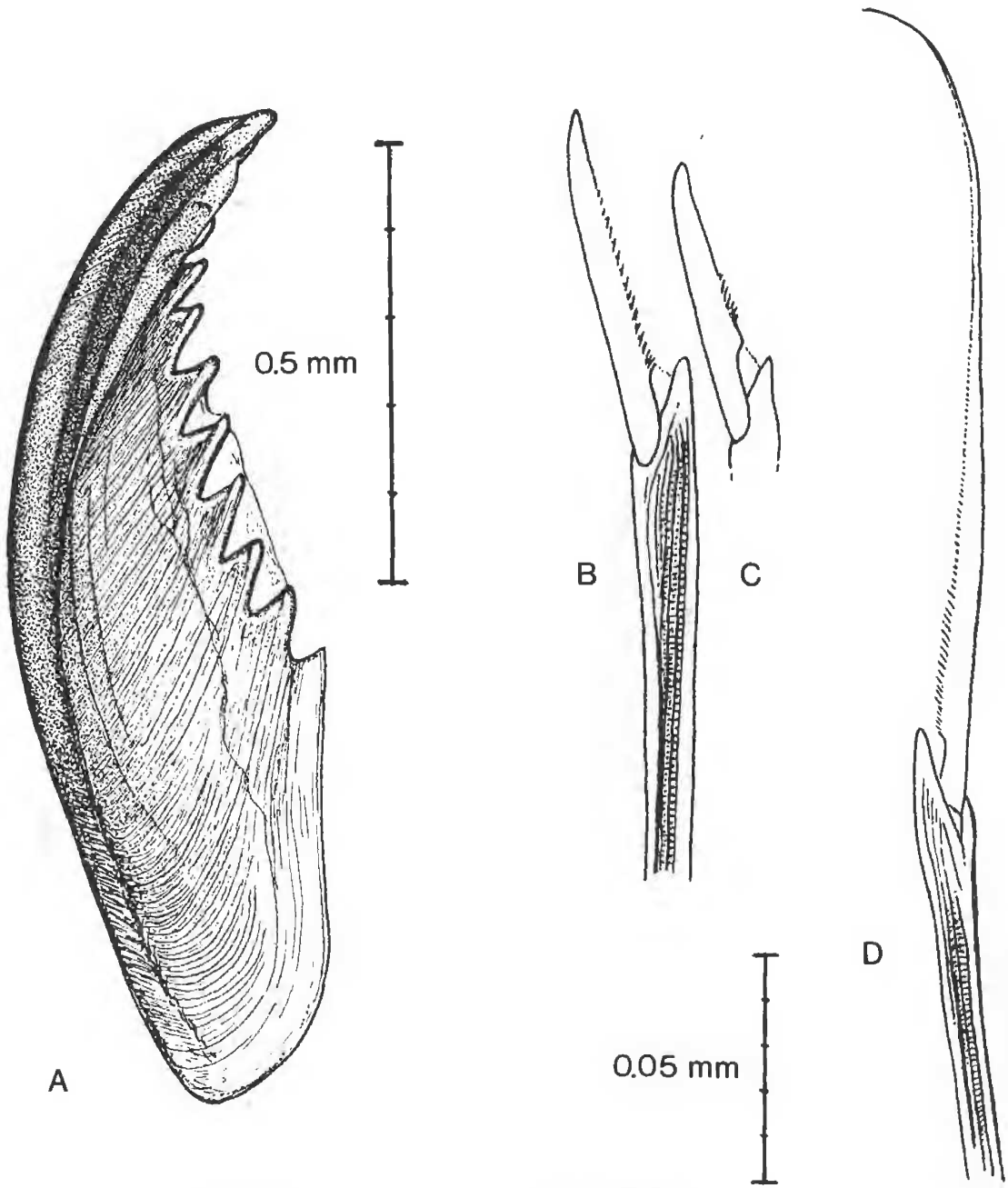


Figure 5. *Namalycastis abiuma*. Sapelo Island, Georgia. A) Right jaw seen from the ventral, concave side, 11 teeth, one hidden by the terminal tooth. From a 70 mm long specimen. B-C) Neuropodial heterogomph falcigers, showing variation in dentation of the blades. D) Neuropodial heterogomph spiniger; all from 24th setiger.

Mature individuals with 11 to 21 neurosetae in each fascicle; neurosetae of two types: heterogomph falcigers, numbering maximally 9 per fascicle, and heterogomph spinigers with up to 12 per fascicle (Figure 5). Highest number of each setal type per fascicle found in the first third of the body, declining in number posteriorly. Any bundle of setae with dominance of spinigers. Heterogomph falcigers with blades finely denticulated, sometimes at base only and of varying lengths (Figure 5B-C). Heterogomph spinigers with long, finely denticulate blade tapering into hairlike tip. Both falcigers and spinigers with dense structure of transverse lamellae in core of shaft, most distinct in falcigers.

The dorsal, longitudinal vessel has a slightly meandering course in the first few segments, with meanders increasing in amplitude considerably toward the posterior end (Figure 4) (normally straight in nereidids (Lindroth, 1938; Nicoll, 1954). The capillary supply is extraordinarily rich in the dorsal part of the posterior segments and in the leaflike, flattened dorsal cirri. Fresh dissection and sectioning of adult worms from Sapelo Island has shown that each segment in the worm body has pulsating "gill hearts" composed of two contractile chambers (Figure 6). Feuerborn (1931) has described such hearts in *Namalycastis ranauensis*; otherwise, they are rarely reported in nereidid worms (Nicoll, 1954).

Biological Observations

N. abiuma was recorded from early November 1971 to January 1972 and February-March 1976, with greatest abundance in fall and winter. It was found under the bark

of rotten pine trunks and branches in or above the ditch water. Heard (1982) also noted the presence of *N. abiuma* in Mississippi living under nearly semi-terrestrial conditions.

Except during the period from November 1971 to March 1972, *N. abiuma* was not observed anywhere in the ditches, not even the mud bottom. All specimens recorded had guts filled with wood pieces (Figures 7-8) and the inside of the surrounding bark had distinct marks made by the jaws of the worms. *N. abiuma* lives freely under the bark and has no permanent tubes; the worms crawled away quickly when bark was removed from the branches. In some cases, they could live semi-terrestrially in the wood pieces since parts of the branches protruded freely in the atmosphere. The worm proved to be a very fast swimmer when released from the wood. It seems likely that the worms under the bark were foraging, perhaps prior to reproduction. All worms taken in November were large, mature individuals with small eggs in their segments. The spring specimens were smaller and without sexual products.

Earlier accounts (Heard, 1982) have established that *N. abiuma* is able to survive under very extreme environmental conditions. At very low oxygen tensions, the posterior end of the worm, with its foliaceous cirri rich in capillary vessels, is seen extended from holes in the bark and waving freely in the surrounding water (aquarium observations, Sapelo Island). This was also observed by Feuerborn (1931, p. 650) for *Lycastis* (*Namalycastis*) *ranauensis* and personally for *Nereis succinea* from Sapelo Island (see below).

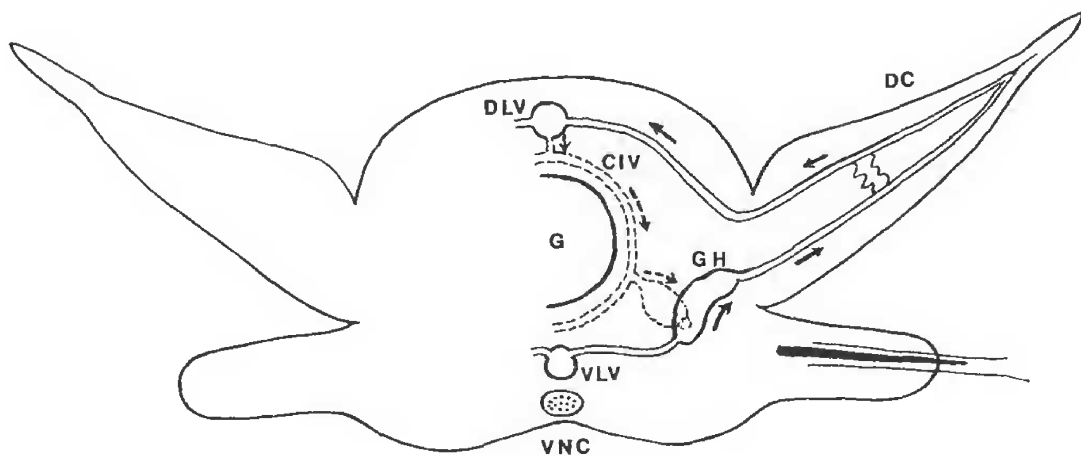


Figure 6. *Namalycastis abiuma* (Müller in Grube, 1971). Schematic diagram of the vascular system showing the main segmental vessels. CIV, circum-intestinal vessel; DC, dorsal cirrus; DLV, dorsal longitudinal vessel; G, gut; GH, gill heart; VLV, ventral longitudinal vessel; VNC, ventral nerve cord.

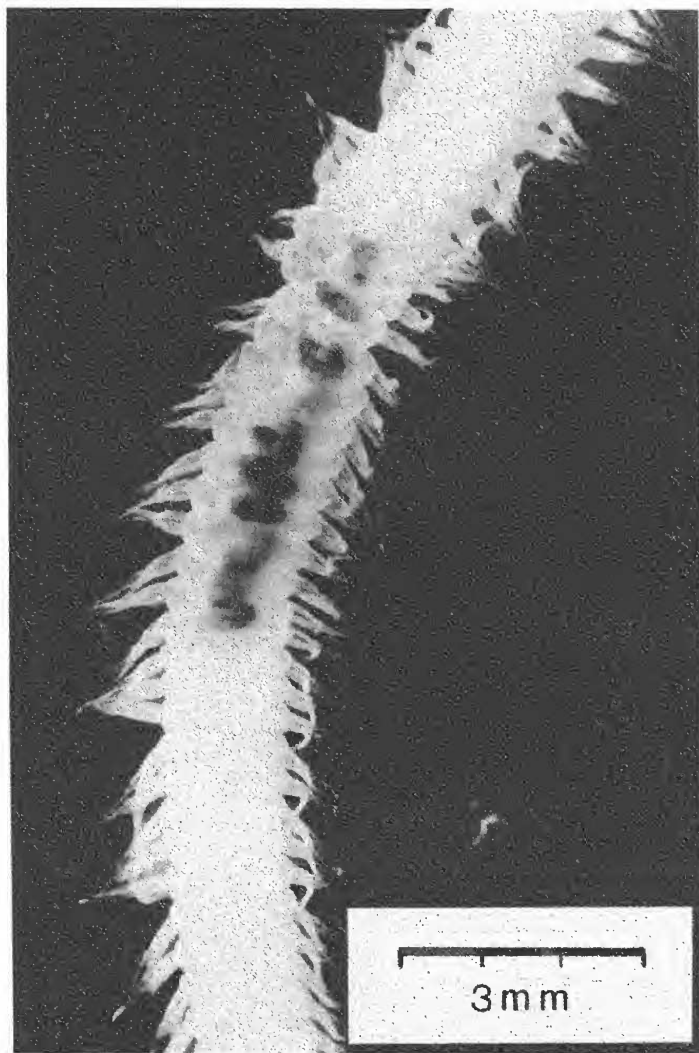
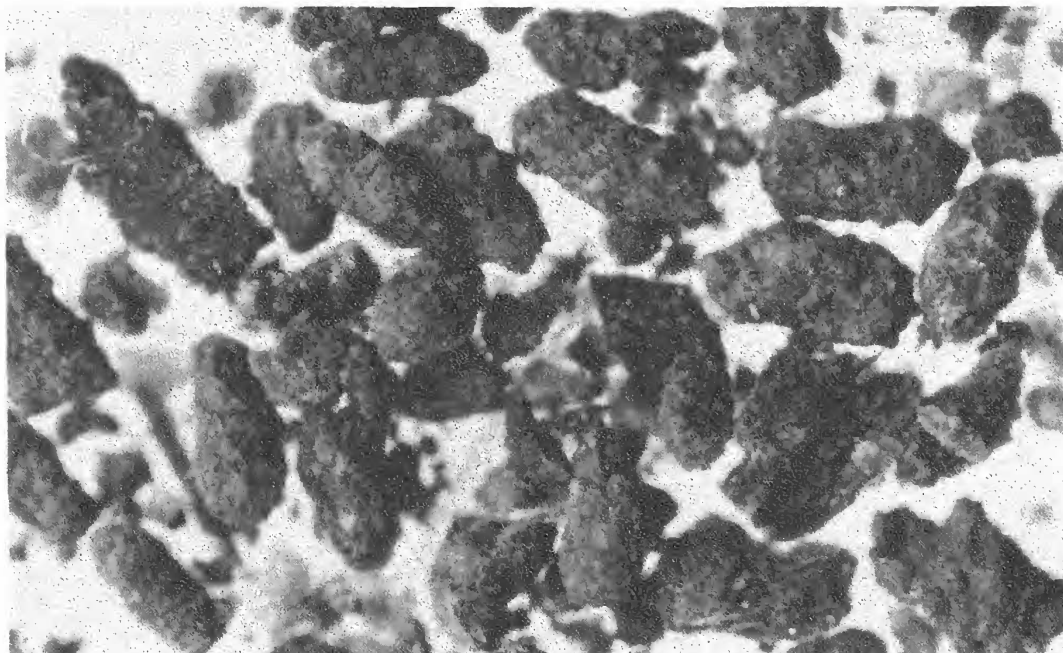


Figure 7. *Namalycastis abiuma*. Sapelo Island, Georgia, November 1971, Station 1. Middle section of adult, preserved specimen with wood and bark pieces in the gut.

Little is known about the reproduction and development of *N. abiuma*. Only small egg cells were observed in the coelom in the material from Sapelo Island (November 1971), and developmental details were not obtained. The only more extensive breeding information for a member of the *Namalycastis* group is given by Feuerborn (1931, Figure 10) for *Lycastis (Namalycastis) ranauensis* from Java. He

found the species to be hermaphroditic with relatively small eggs, 125-135 μ in diameter and laid in a common jelly mass. After about four days the larvae, about 300 μ long, hatched into what Feuerborn described and figured as a ciliated nectochaete stage with three setigers and clearly biramous parapodia. The subsequent fate of the larvae was not described. Because of its freshwater habitat, it seems





 3 mm

Figure 8. *Namalycastis abiuma*. Sapelo Island, Georgia, November 1971. Fecal pellets from adult specimen with remnants of bark and wood particles.

very unlikely that *N. abiuma* has a free-swimming pelagic stage. Only Heard (1982), who kept individuals of *N. abiuma* in aquaria, mentioned large eggs with direct development as the most likely form of propagation of the species, but gave no further information. Otherwise, there are virtually no details of the propagation of other *Namalycastis* species.

Faunal Associations

The survey below comprises benthic species living associated with *Namalycastis abiuma* on or under the bark of dead and windfallen branches mostly of pine trees, predominantly the loblolly pine, *Pinus taeda* L., lying in the brackish water of Sapelo Island ditches.

- ▲ indicates presence under bark and in wood
- △ indicates presence on surface of branches

POLYCHAETA

▲ *Nereis (Neanthes) succinea* (Frey and Leuckart, 1847).

Very common at all examined places, both in 1971-72 and 1976. Often large specimens; maximum length of living animal 170 mm. It burrows under bark and seems to feed on decaying wood. The animals were surrounded by brownish excrement masses, undoubtedly originating from devoured wood remnants. Individuals from March 24, 1976 were almost sexually ripe and in the heteronereid stage. Under low oxygen tensions combined with high water temperatures, the posterior end of the worm, with its many ligules rich in capillary vessels, was seen extended and waving freely in the water (laboratory observations). In case of extreme low oxygen conditions, the species may leave the water and live partly amphibious under the bark of branches exposed to the air.

▲ *Stenonereis martini* Wesenberg-Lund, 1958

This tiny aberrant nereid species is another remarkable member of the decaying wood biotope of the tidal ditches of Sapelo Island. It was found both during 1971-72 and in March-April 1976, frequently in groups of up to six individuals at a time and always in grooves under the bark. All specimens were taken only in the spring in different parts of the ditches. Living individuals measured 7-12 mm. One ripe male specimen was collected on April 16, 1976. The morphology and systematic characters of the examined specimens agree with the description given by Pettibone, 1971.

The species occurs mainly in tropical-subtropical America. Since first described in 1958 by Wesenberg-Lund from St. Martin in the West Indies, it has been recorded from the eastern and northwestern parts of the Gulf of Mexico and from North Carolina. It is known from open water and tidal ponds with great fluctuations in salinity (St. Martin) and penetrates into environments characterized by widely fluctuating conditions: warm mineral springs (Florida), salt marshes (Texas and Mississippi), *Spartina* marsh (North Carolina), and on silt and muddy substrate with little or no oxygen (Hartman, 1958; Pettibone, 1971; Williams *et al.*, 1976; Gardiner and Wilson, 1977; Heard, 1982).

▲ *Polydora ligni* Webster, 1879

Three smaller specimens in mud tubes under pine tree bark.

▲ *Hobsonia florida* (Hartman, 1951)

A single, ca. 12 mm long specimen in mud tube under bark, Bell Marsh ditch system (Station 10), March 28, 1976, salinity 8. The systematic characters agree with the description by Banse, 1979.

CRUSTACEA

△ *Balanus eburneus* Gould, 1841

Fairly common, especially on the undersides of the branches; maximum basic diameter 25 mm. Newly settled individuals present on March 28, 1976 in the Bell Marsh ditch system.

△ *Balanus improvisus* Darwin, 1854

Common, predominantly on the sheltered sides of the branches. On November 11, 1979, numerous small, newly-settled specimens present, less than 1 mm across. On April 23, 1976, pelagic larvae in abundance at Station 1.

▲ *Hargeria rapax* (Harger, 1879) = *Leptochelia rapax* Harger, 1879

1 female with eggs, 3.5 mm long, under bark, Bell Marsh ditch system, March 28, 1976.

▲ *Cyathura polita* Stimpson, 1855

Single specimen under bark, Bell Marsh ditch system, March 28, 1976.

△△ *Cassidinidea ovalis* (Say, 1818) = *C. lunifrons* (Richardson, 1900)

In quantity under bark. From both Station 1 and the Bell Marsh ditch system, where a few individuals were observed crawling on branches. Females with eggs, March 28, 1976.

▲ *Sphaeroma terebrans* Bate, 1866 = *S. desiructor* Richardson, 1897

In quantity under bark and in shipworm-bored branches in all ditches examined.

△△ *Gammarus daiberi* Bousfield, 1969

Adult specimens numerous on and under the park of pine branches, also in wood bored by shipworms, salinity 8‰. Females with eggs, March 28, 1976.

This American endemic species is rather newly described by Bousfield (1969). It has a restricted distribution in estuarine systems from the Delaware and Chesapeake Bay regions south to South Carolina. According to Bousfield, the most dense populations are at salinities of 1-5‰ and in mid-water to near bottom depths. It may be found at 15‰ salinity, then largely pelagic; and development within one year. Oviparous females occur from March to October. Its occurrence on Sapelo Island seems to be the most southern on record.

△△ *Melita nitida* Smith, 1873

Adult specimens (both sexes) common under pine tree bark at Station 1, November 1971 and January 1972. In March 1976 on and in rotten ranches.

△ *Uhlorchestia uhleri* (Shoemaker, 1936)

Often in numbers, crawling on submerged parts of branches close to the water surface.

▲ *Panopeus herbsti* H. Milne-Edwards, 1834

Two young females, carapace width 12 and 13 mm, in empty shipworm tubes.

▲ *Eurytium limosum* (Say, 1818)

Two males, carapace width 5.5 mm, under bark, Station 1, January 20, 1972.

▲ *Sesarma reticulatum* (Say, 1817)

One female, carapace width 7 mm, under bark, Station 1, January 20, 1972.

▲ *Sesarma cinereum* (Bosc, 1801 or 1802)

Common under bark, carapace width 2.5 to 16 mm, Station 1, 1971-72 and 1976.

INSECTA

▲ Chironomid larvae, blood-red species, a few in mud tubes under bark.

▲ Odonata, unidentified species, a single larva under bark; November 11, 1971 at 20‰ salinity.

MOLLUSCA

△△ *Melampus bidentatus* Say, 1822

A few small specimens under bark in water; also observed crawling on submerged parts of the branches.

- ▲ *Geukensia demissa* (Dillwyn, 1817) = *Modiolus demissus* (Dillwyn, 1817)
A few byssally-attached specimens under bark, length about 15 mm.
- △ *Crassostrea virginica* (Gmelin, 1791)
Common on branch surfaces, maximum size 80 mm, many dead shells.
- ▲ *Bankia gouldi* Bartsch, 1908
Fairly common, often in small and thin branch pieces.
- ▲ *Teredo bartschi* Clapp, 1923
Fairly common, often in small and thin branch pieces.

ENTOPROCTA

- △ *Barentsia* sp.
Not very common, on surface of bark in various ditch systems.

ECTOPROCTA

Living colonies of the following species were found in abundance on the surfaces of branches, attached barnacles and oysters.

- △ *Membranipora tenuis* Desor, 1848
- △ *Electra monostachys* (Busk, 1854)
- △ *Conopeum tenuissimum* (Canu, 1928)
- △ *Bowerbankia gracilis* O'Donoghue, 1926
- △ *Alcyonidium polyoum* (Hassall, 1841)
- △ *Victorella* sp.

ASCIDIACEA

- △ *Molgula manhattensis* (De Kay, 1843)
Present, but uncommon, as large specimens on the outer surface of branch pieces.

ACTINIARIA

- ▲ Even one tiny unidentified flesh-colored sea anemone was taken under loose pine bark below sea water.

DISCUSSION

In considering the taxonomic status of *Abiuma*, even generally established systematic characters must be used with care. For example, the position of the eyes of *N. abiuma* may be different according to the condition of the preserved material. In the Sapelo Island material, living worms had the eyes in a transverse row (Figure 4), while they were behind each other in preserved and somewhat shrunken specimens.

An aid in species separation within the genus *Namalycastis* may be offered by possible differences in modes of propagation and development. Hartman (1959, p. 163) mentions one form of the type species (*Paranereis (Namalycastis) abiuma* Müller in Grube, 1871) from Brazil, which was described as having small eggs and separated sexes, with no mention of further development. Another form (*N. ranauensis*) with small eggs,

hermaphroditism, and anectochaete stage (perhaps pelagic) was described by Feuerborn (1931). Both forms were from freshwater. The results of Heard (1982) indicate large eggs and direct development for what he considers to be the type species *N. abiuma* from brackish water. Still rather incomplete, these descriptions, apparently with the same external characters, may suggest three different species at any rate. Further studies on the breeding biology of this aberrant group may provide a clue to the speciation problems within the genus *Namalycastis*.

The ingestion of decaying and rotten wood seems to be unknown for nereidids and perhaps for polychaete worms as a whole (Fauchald and Jumars, 1979). Not only *Namalycastis abiuma* has this peculiar feeding pattern, but *Nereis (Neanthes) succinea* also consumes decaying wood, as shown in this study. It seems reasonable to assume that the fraction of importance for the two species is the microorganisms of the wood.

Off the German coast, *N. succinea* is a deposit-feeder and detritus-feeder (Goerke, 1971). *N. abiuma* may also be a deposit-feeder in other parts of its range of distribution. Thus their diets may vary greatly and both may be characterized as omnivores. However, as pointed out by Fauchald and Jumars (1979, p. 255), "...a widely dispersed species feeds on a limited range of materials, indicating that, while the species as a whole may be omnivorous, each population may be functionally specialized."

The fauna associated with *N. abiuma* in or on fallen branches in the ditch water comprises 34 benthic species. Apart from the two freshwater insects, the remaining are brackish-water, estuarine or euryhaline marine species. There is a clear dominance of crustaceans with 13 species, followed by five polychaetes, five molluscs, and six ectoprocts (bryozoans).

ACKNOWLEDGMENTS

Special thanks are expressed to Professor V.J. Henry, former director of the University of Georgia Marine Institute, for arranging my visit in 1971-72 as a staff member at the station. Thanks are also extended to all personnel for their kind help and assistance during my visits. I am indebted to Professor W.D. Burbanck and the late Professor Ralph I. Smith for helpful comments in reviewing the manuscript, and to Professor C. Overgaard Nielsen for correcting and revising the manuscript. I am indebted to the following experts for their aid in the identification work: Dr. J. Just, Zoological Museum, Copenhagen; Dr. R. Turner, Museum of Comparative Zoology, Harvard University; Dr. K.B. Hansen, Zoological Museum, Copenhagen; and Dr. Patricia Kott, Queensland Museum, Australia. Lastly, I would like to acknowledge financial support provided by the Danish Natural Science Research Council and the Carlsberg Foundation.

The material collected is deposited in the Zoological Museum, Copenhagen.

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